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On cell assemblies in a cortical column

Friedrich T. Sommer*

Department of Neural Information Processing, University of Ulm, D-89069 Ulm, Germany

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Abstract

Recent experimental evidence for temporal coding of cortical cell populations (Riehle, Grün, Diesmann, Aertsen, Science 278 (1997) 573–578, Donoghue, Sanes, Hatsopoulos, Gaál, J. Nuerophysiol. 79 (1998) 159–173). recurs to Hebb's classical cell assembly notion. Here the properties of columnar cell assemblies are estimated, using the assumptions about biological parameters of Wickens and Miller, Biol. Cybernet. 77 (1997) 351–358, but extending and correcting their predictions: Not the combinatorical constraint as they assume, but synaptic saturation and the requirement of low activation outside the assembly limit assembly size and number. As will be shown, (i) columnar assembly processing can be still information theoretically efficient, and (ii) at efficient parameter settings several assemblies can be ignited in a column at the same time. Feature (ii) allows faster and more flexible access to the information contained in the set of stored cell assemblies.

Keywords: Population coding; Associative memory; Hebbian synapses

1. Introduction

The cortical representation of psychological concepts, situations and actions by population coding is an old idea [4]. Hebb [3] postulated the representation of concepts by coactivation in *cell assemblies*, and suggested a simple local synaptic mechanism how the brain could learn concepts. Recent experiments [7,1] support the so-called temporal coding assumption, that is, population coding through coincident single spike events, rather than coding through firing rates [2]. In this, picture cortical γ-oscillations can be interpreted as sequences of (spacially coded) cell assemblies: simulations with compartment neurons have shown that cell assemblies stored by Hebbian learning can be recalled as synchronious spike patterns at high information

* Tel.: + 0049-731-502-4154; fax: + 0049-731-502-4156.
E-mail address: Friedrich.Sommer@informatik.uni-ulm.de (F.T. Sommer).

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capacity and with maximum readout frequencies lying in the γ-band [8]. This paper investigates possible spacial properties of cell assemblies within a cortical column. Extending previous works [5,6,9] we determine analytically possible operation ranges of cell assembly processing from the known anatomical and electrophysiological parameters. Finally, multi-assembly ignition will be examined: a parameter range where several activated assemblies can coexist allows for a richer repertoire of memory access, in particular, sequential recall in the γ-band, given the typical low-time constants of integration effects involved.

2. Model assumptions and parameter estimation

Hebb [3] postulated that cells in assemblies have a strong mutual connectivity providing that activation of a whole assembly is self-sustaining, and can be stimulated from a subset of cells. The following analysis will examine the possible properties of intracolumnar cell assemblies using the assumptions from an earlier paper [9]: the activation of a columnar neuron is described by $x_j = H(\sum_i C_{ij}x_i - \theta)$, where $x_j = 1$ or $x_j = 0$ means an action potential/silence of the neuron, C is the synaptic connectivity, θ the *excitation threshold*, and $H(x)$ the Heaviside function. The cell assemblies are assumed as random choices of k cells in the column, and the synaptic storage is described by binary clipped Hebbian learning, where for M learned assemblies $P = 1 - (1 - k^2/n^2)^M$ gives the *synaptic modification probability*. The anatomical connection density is modeled by an independent variable Z_{ij} with $P_s = P[Z_{ij} = 1]$. Thus, synaptic values are given by $C_{ij} = Z_{ij} \sup_{v=1,\ldots,M} x_i^v x_j^v$ with $P[C_{ij} = 1] = P_s P$. *Ignition* of an assembly will be considered using initial stimulation at a subset kf of assembly neurons, $0 < f \leq 1$ is called the initial fraction. As model parameters estimated from biological data we choose the values in Table 1, taken over from [9].

Our analysis will derive possible (and efficient) cell assembly parameters, like assembly size (k), the number of assemblies (M) and ignition fraction (f).

3. Analysis of assembly learning and assembly ignition

What are the conditions that local cell assemblies can be learned and recalled? The condition on the learning process is that the resulting synaptic structure has to reflect

Table 1
Properties of excitatory neurons in a column. The lower three lines yield the excitation threshold of a neuron in terms of excitatory postsynaptic potentials (EPSP): $\theta = 5$–50

Volume of cortical column	1 mm^3
Excitatory neurons in volume	$n = 90\,000$
Anatomical connectivity	$P_s = 0.1$
Resting membrane potential	-74 ± 5 mV
Cell firing threshold	-50 mV
Unitary EPSP size (typical range)	0.5–2 mV

properties of the cell assemblies. For $P = 0.5$ *optimal learning* is provided, i.e., the Shannon information in the synapses becomes maximal. Increasing the load, for $P > 1 - 1/(n^2 P_s)$ *synaptic saturation* is reached, i.e., the expectation on the number of synapses that remain unchanged drops below one, and the synaptic structure just corresponds to the anatomically precent synapses but contains no information about the assemblies. The opimal learning condition and the synaptic saturation bound are given by $M^{\mathrm{ol}}(k,n) = -\log[2]/\log[1-k^2/n^2]$ and $M^{\mathrm{ss}}(k,n) = M^{\mathrm{ol}}(k,n)\log[P_s n^2]/\log[2]$.

Further conditions have to ensure the success of assembly recall by the ignition process. *Combinatorical restriction:* If the initial fraction f is large enough to ignite the assembly it will also ignite all other assemblies that contain the initial fraction too. Thus, the number of stored assemblies has to be restricted in order to keep the probability of high mutual overlaps between assemblies (larger or equal to $f_{\min}k$) small. In [9] the expectation number of high mutual overlaps was required to stay below one. We use this condition and denote the resulting bound M^{c} as the combinatorical bound

$$\left(1 - \sum_{r=0}^{f_{\min}k} \binom{k}{r}\binom{n-k}{k-r}\binom{n}{k}^{-1}\right)\frac{M^{\mathrm{c}}(M^{\mathrm{c}}-1)}{2} = 1.$$

Safe assembly ignition: Excitation of a neuron depends on the former network activity. If a_{in} neurons are active in assemblies where the neuron is member and a_{out} neurons outside, the excitation probability is

$$P_{\mathrm{ex}}(a_{\mathrm{in}}, a_{\mathrm{out}}) = 1 - \sum_{r=0}^{\theta-1}\sum_{s=0}^{r} B(a_{\mathrm{in}}, s, P_s)B(a_{\mathrm{out}}, r-s, P_s P) \tag{1}$$

with the Binomial distribution $B(n,r,p) = \binom{n}{r}p^r(1-p)^{n-r}$.

We consider assembly ignition from an initial fraction f. If l assemblies with average mutual overlap are stimulated simultaneously with initial fractions f the initial activity is almost lfk ($l = 1$ describes ignition of a single assembly, as usually considered). Using (1) the probability of excitation of a neuron is $P_{\mathrm{in}}(f,k,l) = P_{\mathrm{ex}}(fk,(l-1)fk)$ within ignited assemblies and $P_{\mathrm{out}}(f,k,l) = P_{\mathrm{ex}}(0,lfk)$ outside. The assembly will be ignited safely, if (i) the initial activity is larger than

$$f_{\min}(k,l) = \min_{f}\{P_{\mathrm{in}}(f,k,l) \geq f\}$$

cf. [9], and if (ii) ignition can be kept inside ignited assemblies, i.e., the outside/inside excitation ratio $e(k,l)$ stays below a small bound τ. The second condition defines another bound on the the number of assemblies in the volume, the *safe ignition* bound

$$M^{si}(f_{\min},k,l,\tau) = \max_{M}\{e(k,l) < \tau\}, \quad e(k,l) = \frac{(n-k)P_{\mathrm{out}}(f_{\min},k,l)}{kf_{\min}}.$$

Note that P_{out} and for $l > 1$ also $f_{\min}$ depend over P on the parameter M.

4. Results

In the following diagrams solid lines show the quantities marked on the individual y-axis as functions of the logarithmic assembly size k. The parameter values for n and P taken from Table 1.

4.1. Ignition of one cell assembly ($l = 1$)

Figs. 1–3 display results for four different neuronal excitation thresholds. The curves are labeled in Fig. 1 (left) and can be identified in the other diagrams by the onset points that are in the same order from left to right.

Fig. 1 specifies initial patterns providing assembly ignition: they lie above the solid curves and below $f = 1$, displayed in the right diagram by the dashed line. The minimal ignition activity slightly diminishes with assembly size because of the decrease of the relative threshold.

Fig. 2 (left) shows the safe ignition bounds. For small assembly sizes they stay below the optimum learning condition, for large sizes they exeed it, but clearly, they are more restrictive than the synaptic saturation bound. Fig. 2 (right) shows the combinatorical bounds. They become only relevant for very large assembly sizes and taking into

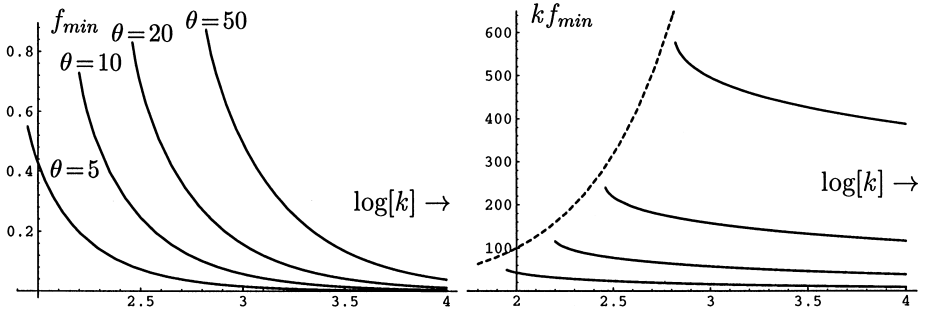

Fig. 1. Minimal ignition fraction (left) and initial activity (right).

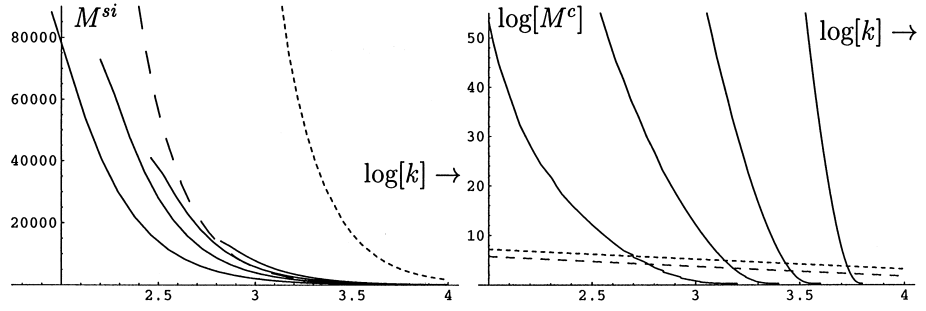

Fig. 2. Safe ignition bounds for $\tau = 0.1$ (left) and combinatorical bounds (right). Long dashes: M^{ol}, short dashes: M^{ss}.

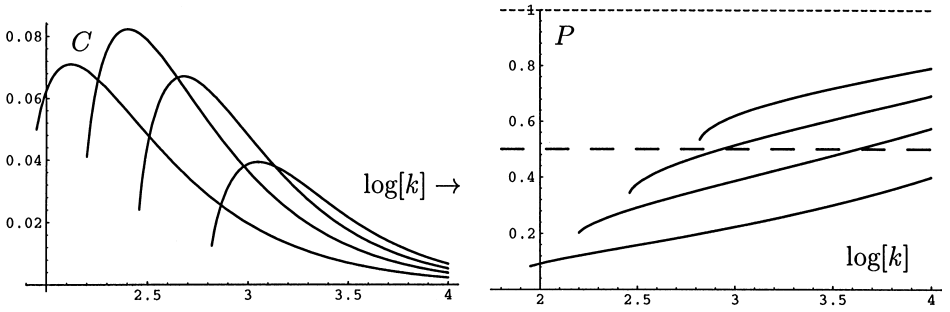

Fig. 3. Columnar information capacity and corresponding synaptic modification probabilities (right) for $\tau = 0.1$. Long dashes: P^{ol}, short dashes: P^{ss}.

account them only wrongly predicts operation ranges far beyond synaptic saturation, like the parameter constellation $M = n$ at assembly sizes $k = 1400$ described in Ref. [9].

Fig. 3 (left) shows the information capacity achieved with safe ignition in bits per synapse using $C = MI_g/(n^2P_s)$ where I_g is the mean information gain per assembly provided by the ignition process [8]. The parameter constellations at the information maxima are given in Table 2. Note in Fig. 3 (right) that in general maximum capacity does not coincide with optimal learning.

The overall information capacity maximum is of the order of magnitude of the theoretical optimum ln[2]/4 — about half of it.

4.2. Multi assembly ignition

Fig. 4 (left) shows the effects of mutual excitation for multi assembly ignition: the minimal overall initial activity scales sublinearly in l, and the safe ignition constraint drops with the number of ignited assemblies l. Fig. 4 (right) indicates that for fewer and larger assemblies multi assembly ignition is possible with reasonable high information

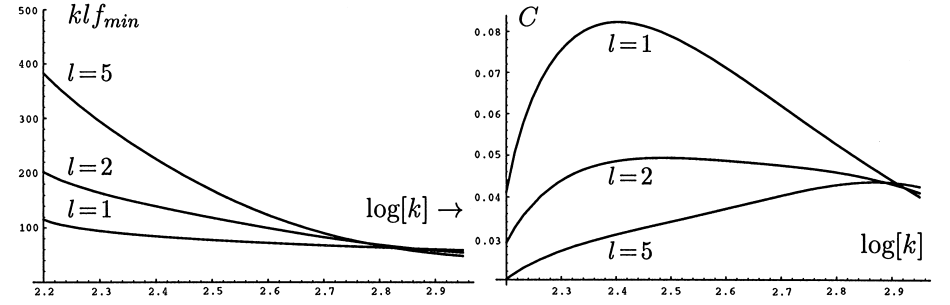

Fig. 4. Minimal ignition activity and information capacity for multi assembly ignition with $l = 1,2,5$ assemblies at an excitation threshold $\theta = 10$ and again $\tau = 0.1$.

Table 2
Efficient parameter sets. The optimal assembly size and number varies for different neuronal excitation threshold values but variation of the best ignition fraction f is moderate. The overall capacity optimum is reached for an excitation threshold near $\theta = 10$

θ	5	10	20	50
k	120	250	500	1200
M	64 000	40 000	16 000	8000
f	0.3	0.34	0.38	0.48
kf	36	87	190	460
C	0.071	0.082	0.068	0.04

capacity: For $l = 5$, efficient parameters are $k = 800$ and $M = 10\,000$ where during ideal ignition the activity spreads from 100 to 4000 cells. At final activity the average input at an outside neuron is $klPP_s \simeq 16$. Thus, uncontrolled activity spread has to be prevented by a dynamical threshold alignment, for instance, through inhibitory cells.

5. Conclusions

Estimations on cell assembly properties in a cortical column (in particular, the size and number, see Table 2) have been derived from biological constraints (Table 2). Further, the analysis predicts the possibility of multi-assembly ignition, an extended mode to access the synaptically stored information in the cortex.

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